# From sharing food to sharing information: Cooperative breeding and language evolution

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Abstract: Language is a cognitively demanding human trait, but it is also a fundamentally cooperative enterprise that rests on the motivation to share information. Great apes possess many of the cognitive prerequisites for language, but largely lack the motivation to share information. Callitrichids (including marmosets and tamarins) are highly vocal monkeys that are more distantly related to humans than great apes are, but like humans, they are cooperative breeders and all group members help raising offspring. Among primates, this rearing system is correlated with proactive prosociality, which can be expressed as motivation to share information. We therefore propose that the unique coincidence of these two components in humans set the stage for language evolution: The cognitive component inherited from our great ape-like ancestors, and the motivational one added convergently as a result of cooperative breeding. We evaluate this scenario based on a review of callitrichd vocal communication and show that furthermore, they possess many of the mechanistic elements emphasized by the mirror system hypothesis of language evolution. We end by highlighting how more systematic phylogenetic comparisons will enable us to further promote our understanding of the role of cooperative breeding during language evolution.

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# From sharing food to sharing information. Cooperative breeding and language evolution

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## ABSTRACT

Language is a cognitively demanding human trait, but it is also a fundamentally cooperative enterprise that rests on the motivation to share information. Great apes possess many of the cognitive prerequisites for language, but largely lack the motivation to share information. Callitrichids (including marmosets and tamarins) are highly vocal monkeys that are more distantly related to humans than great apes are, but like humans, they are cooperative breeders and all group members help raising offspring. Among primates, this rearing system is correlated with proactive prosociality, which can be expressed as motivation to share information. We therefore propose that the unique coincidence of these two components in humans set the stage for language evolution: The cognitive component inherited from our great ape-like ancestors, and the motivational one added convergently as a result of cooperative breeding. We evaluate this scenario based on a review of callitrichd vocal communication and show that furthermore, they possess many of the mechanistic elements emphasized by the mirror system hypothesis of language evolution. We end by highlighting how more systematic phylogenetic comparisons will enable us to further promote our understanding of the role of cooperative breeding during language evolution.

## 1) INTRODUCTION

The communicative abilities of extant primates can crucially inform our understanding of language evolution. In the predominant approach, researchers identify elements of language in primates that are more or less closely related to humans, to infer if these elements had likely been present in the corresponding last common ancestor. The big brained great apes, our closest relatives, appear endowed with many of the cognitive prerequisites for language (as perhaps most evident in language trained apes: Tomasello 2017), which therefore most likely were already present in the last common ancestor of humans and other great apes. Other elements of language seem largely lacking in the great apes, perhaps most fundamentally the motivation to share information which is beneficial to others rather than themselves (see also Wacewicz, Zywiczynski & Chiera, this issue). For instance, even language trained great apes use their communicative skills almost exclusively imperatively (Tomasello, 2008, 2017); in other words, they mostly lack the motivation to share information (Fitch, 2005).

Elements of language that are absent in our closest relatives cannot be explained through shared ancestry. They may be uniquely present in humans, or else present in less closely related species. In the latter case, an evolutionary approach that is complementary to identifying shared ancestry becomes possible, i.e. to ask whether these traits may be the result of convergent evolution, and their presence in some species but not in others linked to specific social or ecological factors.

One factor that has played a convergent role during human evolution is cooperative breeding, which has considerable explanatory power for understanding numerous features of our life history, demography, and cognitive endowment (Burkart, Hrdy, & van Schaik, 2009; Hrdy, 2005b, 2009). Cooperative breeding refers to a social system in which not only the parents provide care for the offspring (Solomon & French, 1997). Among primates, callitrichid monkeys (i.e. marmosets, tamarins, and callimicos) and humans are the only species known to show such a social system. In callitrichids, all group members cooperate in raising offspring by carrying and later provisioning the immatures (Digby, Ferrari, & Saltzman, 2007), and they frequently cooperate also in a variety of other activities including territory defense, vigilance, anti-predator behavior or food harvesting (Garber, 1997). The infants are continuously carried during the first weeks of life, which requires high levels of coordination among all group members (Snowdon, 2001). During provisioning, they regularly engage in proactive food sharing, i.e. unsolicited sharing initiated by the possessor. This is common in all human societies and callitrichid monkeys, yet virtually absent in all great ape and most monkey species. In these other species, if food is shared at all, it is mostly shared passively

(tolerated taking) or in response to begging and requests and thus initiated by the potential recipient, rather than by the possessor and his or her motivation to share (Brown, Almond, & van Bergen, 2004; Jaeggi, Burkart, & van Schaik, 2010; Melis & Warneken, 2016). Systematic comparative evidence from 24 groups of 15 primate species indicates that the prosocial motivation to share food is linked to cooperative breeding in primates (Burkart et al., 2014; see also Horn et al. 2017 for a similar pattern in corvids). This prosocial motivational predisposition is also reflected in other cooperative interactions. During cooperative problem solving, for instance, callitrichid monkeys continue to contribute to the task even if for some time, they don't receive a reward for cooperating, whereas independently breeding primates such as chimpanzees, orangutans or capuchin monkeys quickly decrease their cooperative contributions (Snowdon & Cronin, 2007). Thus, cooperation per se is not unique to callitrichid monkeys, but it is more frequent and more often based on prosocial rather than individualistic and selfish motives compared to independently breeding primates.

The working hypothesis put forward in this paper is that human language evolution was enabled on the one hand, because our hominin ancestors had inherited from their great ape ancestors many of the cognitive prerequisites for language. On the other hand, they were also equipped with the prosocial motivational component, and this is better understood as a consequence of cooperative breeding that evolved in our hominin ancestors but in none of the other extant great apes. Thus, these two components per se are not unique to humans, but the coincidence of both components in the same species is, and may explain why language evolved in the human lineage, rather than in any other (ape) species.

The cooperatively breeding callitrichid monkeys give us the opportunity to investigate the consequences of cooperative breeding and a more prosocial attitude on communicative complexity per se (Borjon & Ghazanfar, 2014; Burkart & van Schaik, 2016; Hrdy, 2005a; Snowdon, 2001; Zuberbühler, 2011). They are small New World primates who shared a last common ancestor with humans more than 37-54 million years ago, and they lack the big and powerful brains of great apes. The goal of this article is to evaluate the hypothesis that there may be a link between cooperative breeding and communicative complexity, by first reviewing callitrichid vocal communication and examining how this evidence fits with specific potential pathways through which cooperative breeding may be linked to communicative complexity. We will then turn to the mirror system hypothesis and show that callitrichids indeed possess many of the mechanistic elements proposed by this hypothesis, and finally propose how more controlled phylogenetic approaches will help us to systematically test the link between cooperative breeding and language evolution.

## 2) CALLITRICHID VOCAL COMMUNICATION

The communicative system of callitrichids appears unusual among nonhuman primates (Rukstalis, Fite, & French, 2003; Snowdon, 2013). They are highly voluble monkeys that vocalize almost constantly (Eliades & Miller, 2016), have large vocal repertoires for nonhuman primates (Agamaite, Chang, Osmanski, & Wang, 2015; Campbell & Snowdon, 2007; Cleveland & Snowdon, 1982; Masataka, 1982; McComb & Semple, 2005), and frequently produce a variety of call combinations (Agamaite et al., 2015; Bezerra & Souto, 2008; Cleveland & Snowdon, 1982). The structure of callitrichid vocalizations encodes information about group, sex, and individual identity, and recipients can discriminate at least the latter (Rukstalis & French, 2005; Weiss, Garibaldi, & Hauser, 2001).

Individuals sometimes engage in cooperative turn-taking where partners flexibly adjust the timing of their vocalizations to each other (Takahashi, Narayanan, & Ghazanfar, 2013), both in dyadic and polyadic situations (Snowdon & Cleveland, 1984). Turn-taking occurs when individuals are separated, and they start calling back and forth with the other group members (using *phee*-calls; for qualitative differences between callitrichid and human turn-taking, see Wacewicz et al., this issue). Artificial playbacks of interfering noise during turn-taking exchanges suggest considerable vocal control over the timing (Roy et al. 2011). When noise was played back at predictable intervals, the monkeys would time their calls such that the first call would occur in the first silent interval and the answer only after the next bout of noise in the subsequent silent interval. Alternatively, call and answer were emitted with a shortened latency to fully fit within a predictable period of silence.

Some of the calls of callitrichids are functionally referential, referring to predators (Cäsar & Zuberbühler, 2012; Kirchhof & Hammerschmidt, 2006) and also to food (Kitzmann & Caine, 2009). Food calls occur in several primate species and can have various functions (Clay, Smith, & Blumstein, 2012). They can be emitted selfishly and indicate ownership of a specific food source. Capuchin monkeys, for instance, are more likely to emit food calls when others are present, and less likely to be approached by others when emitting food calls (Gros-Louis, 2004; Pollick, Gouzoules, & de Waal, 2005). Food calls can also function to attract others to big, sharable food source like a fruiting tree in order to reduce predation rather than to share food. In callitrichids, finally, food calls can function to attract others in order to offer food to them, when during proactive sharing, food possessors first emit food offering calls and then wait with food in their outstretched hands for immatures to come and take it (Brown et al., 2004). Accordingly, adult callitrichids are more likely to

call when others are absent rather than present (Caine, Addington, & Windfelder, 1995; Vitale, Zanzoni, Queyras, & Chiarotti, 2003). Callitrichid food calls are to some extent independent of the caller's own feeding motivation, because adults are more likely to call if immatures are present in the group (Guerreiro Martins, Moura, Finkenwirth, & Burkart, in rev,), and when immatures are unable to obtain food independently from a puzzle box that only the adult can open (Guerreiro Martins & Burkart, 2013; Moura, Nunes, & Langguth, 2010).

As in other nonhuman primates, the vocabulary in callitrichds is fixed, and no novel vocalizations are acquired via vocal learning. Nevertheless, some flexibility appears present. The acoustic structure of vocalizations differs considerably between populations (de la Torre & Snowdon, 2009; Zuercher & Burkart, 2017), and translocation experiments show that these differences are indeed the result of vocal production learning rather than environmental or genetic differences (Zuercher & Burkart, in prep). This kind of vocal accommodation, i.e. changes in the structure of a given vocalization in response to social factors, has been reported in several other primate species too and serves the function of indicating social closeness (Ruch, Zürcher, & Burkart, 2017). Social influences on vocal development during ontogeny, however, seem particularly prevalent in callitrichids (Snowdon, 2017b). For instance, immatures lacking adult vocal feedback because they had been socially deprived (Gultekin & Hage, 2017) or deafened (Roupe, Pistorio, & Wang, 2003) appeared unable to develop proper adult vocal repertoires and were less likely to use certain call combinations.

Callitrichid infants babble, which to our knowledge has not been described in any other primate species except humans. Babbling bouts are noisy and can last up to one minute or more, and consist of strings of elements of calls from the adult repertoire (Elowson, Snowdon, & Lazaro-Perea, 1998b; Pistorio, Vintch, & Wang, 2006). During babbling bouts, adults are more likely to interact with the infants, and infants who babble more produce well-formed adult calls earlier during ontogeny (Elowson, Snowdon, & Lazaro-Perea, 1998a; Snowdon & Elowson, 2001; Takahashi, Fenley, & Ghazanfar, 2016; Takahashi et al., 2015). These findings are complemented by experimental evidence that confirms that contingent parental feedback speeds up vocal development in common marmosets (Takahashi et al., 2016, 2017). In fact, some instances of parental feedback may even satisfy the criteria for teaching (according to the functional definition by Caro & Hauser, 1992), for instance when during turn-taking, parents add an extra break when infants get the timing wrong and respond too quickly, or when infants respond with the wrong call and parents interrupt them with the correct answer, i.e. a *phee*-call (Chow, Mitchell, & Miller, 2015; Takahashi et al., 2016).

## 3) COOPERATIVE BREEDING AND VOCAL COMPLEXITY?

There are at least three, mutually non-exclusive ways in which cooperative breeding in primates may facilitate the emergence of more diverse and more sophisticated forms of communication (Table 1). First and most importantly, the readiness to share food may extend toward a willingness to share information as well. Cooperative breeding may thus have favored the evolution of human language by adding a key element, i.e. the motivation to share information (Fitch, 2005; Grice, 1975; Noble, 2000; Tomasello, 2008), to the cognitive endowment of the last common ancestor that we had shared with the other great apes. In callitrichids, information donation is apparent in food offering calls that function to attract others to a food item (Brown et al., 2004), but also when parents correct immatures in turn-taking sequences where immatures get the timing wrong or choose the wrong call type to answer (Chow et al., 2015). Another form of information donation is teaching. For callitrichids, more evidence consistent with teaching is available compared to independently breeding primates, where teaching appears virtually absent (Kline, 2014). In callitrichids, both in the wild and in captivity, adults have repeatedly been shown to change their behavior in the presence of naïve immatures in a way that is beneficial to skill acquisition in cotton-top tamarins (Humle & Snowdon, 2008; Snowdon & Roskos, 2017), lion tamarins (Rapaport, 2011) and common marmosets (Dell'Mour, Range, & Huber, 2009; Chow, Mitchell, & Miller, 2015; Takahashi et al., 2016, Guerreiro Martins & Burkart, in prep.). The only context in which information donation appears to occur in a wider range of species are alarm calls; they may easily evolve because small costs can have enormous inclusive fitness benefits, but may also be driven by direct fitness benefits (predator deterrence: Shelly & Blumstein 2004) and therefore not represent a case of genuine information donation.

Second, since cooperative breeders routinely engage in a variety of cooperative activities on a daily basis, they may experience more contexts in which they have to coordinate and negotiate with other group members (Snowdon, 2001). For instance, individuals have to coordinate who will engage in infant carrying and who in vigilance or even group defense, because these activities are usually not performed simultaneously. Likewise, the timing of transfers from one caregiver to the next has to be coordinated. An obvious way to meet such increased needs for coordination and social monitoring in arboreal species with limited visibility is through the acoustic channel. The high prevalence of vocalizations emitted in callitrichid groups and their large vocal repertoires are consistent with this pathway. Intriguingly, birds appear to fit this pattern too since cooperatively

breeding species have larger vocal repertoires compared to independently breeding ones (Leighton 2017). Vocal turn-taking (Table 1), finally, is also consistent with this pathway, because it likely scaffolds behavioral coordination by facilitating the monitoring of group members.

Third, selective pressure may also be on immatures in cooperative breeders (Chisholm, 2003; Hawkes, 2014; Hrdy, 2009; Tomasello & Gonzalez-Cabrera, 2017; Zuberbühler, 2011), because they arguably have to engage caregivers who are not their mothers. Furthermore, they may even have to engage their own mothers because maternal investment tends to be conditional in cooperative breeders, and a mother may only properly care for their offspring if she perceives the availability of sufficient allomaternal support (Bardi, Petto, & Lee-Parritz, 2001; Hrdy, 2016). Immatures in cooperative breeders may therefore be particularly selected for attracting caregivers, which may have facilitated the emergence of socio-cognitive skills, including vocal behavior that advertises the immatures' neediness (Chisholm, 2003; Hawkes, 2014; Hrdy, 2009; Tomasello & Gonzalez-Cabrera, 2017; Zuberbühler, 2011). The conspicuous babbling behavior of callitrichids may well fulfil this function. Immature callitrichids are very small and vulnerable to predation, and it is thus unexpected that they frequently vocalize loudly rather than behaving more cryptically. An alternative, but likewise intriguing possibility is that babbling is a simple by-product of large repertoires of which the fine acoustic structure has to be learned during ontogeny (see above).

**Table 1.** Potential, non-mutually exclusive pathways that may link extensive cooperative breeding (reliance on allomaternal care) and vocal complexity.

| Pathway | Elements of callitrichid vocal communication consistent with the pathway |
|---|---|
| ***Propensity to share food extends to propensity to also share information*** | • Food offering calls function to share information that is beneficial for the recipient[1]<br>• Adults are more likely to give food offering calls and share food when immatures lack the skills to obtain food independently[2-4]<br>• Potential teaching by adult marmosets during vocal development of immatures[5-7]<br>• Potential teaching in instrumental contexts[3, 8-10] |
| ***Increased need for coordination & monitoring*** | • Large repertoires and volubility[11-14, see also 15 for birds]<br>• Turn-taking as cooperative vocal exchanges[16] likely to facilitate coordination and mutual monitoring<br>• Turn-taking also follows conversational patterns in polyadic situations[17] |
| ***Engaging caregivers*** | • Callitrichid infants engage in babbling behavior[18, 19]<br>• During babbling, caregivers are more likely to interact with infants[20, 21] |

*Notes.* [1]Brown et al. 2004, [2]Moura et al. 2010, [3]Humle & Snowdon 2008, [4]Guerreiro Martins et al. 2013, [5]Chow et al. 2015, [6]Takahashi et al. 2016, [7]Takahashi et al. 2017, [8]Rapaport 2011, [9]Guerreiro Martins & Burkart in prep, [10]Snowdon & Roskos 2017, [11]McComb & Semple 2005, [12]Cleveland & Snowdon 1982, [13]Campbell & Snowdon 2007, [14]Masataka 1982, [15]Leighton 2017, [16]Takahashi et al. 2013, [17]Snowdon & Cleveland 1984, [18]Elowson et al. 1998, [19]Pistorio et al. 2006, [20]Snowdon 2017, [21]Snowdon & Elowson 2001.

Our first review of data thus suggest that these three, non-mutually exclusive pathways for a potential link between cooperative breeding and communicative complexity in primates are plausible. However, to fully evaluate them, more systematic data for a broad range of primates is critical.

## 4) CALLITRICHID COMMUNICATION AND THE MIRROR SYSTEM HYPOTHESIS

The mirror system hypothesis as an evolving framework (Arbib, 2012) provides an account of the emergence of language at the mechanistic level and stresses the importance of mirror neurons and imitation, intentionality, and brain coupling. In the following section, we summarize studies suggesting that callitrichids in fact possess several of these mechanistic elements.

First, mirror neurons are not unique to Old World primates but have also been demonstrated in common marmosets (Suzuki et al., 2015). Furthermore, marmosets engage in so-called true imitation, defined as the faithful copying of a novel technique with a high degree of matching of the precise actions between the model individual and the observer (Voelkl & Huber, 2007). This is unusual among nonhuman primates (Snowdon, 2017a), but note that this kind of imitation appears restricted to single actions, whereas the exact copying of entire action sequences may well be absent in callitrichids, perhaps due to limitations in working memory (which tends to be correlated with brain size in primates: Burkart, Schubiger, & van Schaik, 2017; see also Aboitiz & Putt, this issue).

Second, social learning not only appears pervasive among callitrichids (Snowdon, 2017a) but it also relies on intention attribution. Specifically, common marmosets have been shown to only engage in social learning from intentional agents, i.e. agents that they perceive to behave in a goal-directed way (Burkart, Kupferberg, Glasauer, & van Schaik, 2012; Kupferberg, Glasauer, & Burkart, 2013). In habituation-dishabituation experiments, marmosets were first shown to perceive the behavior of approaching one of two objects as goal-directed. They did so if the behavior was performed by a conspecific, a human actor, and to a lesser extent by a robot, but not if performed by a black box. Rather, if performed by the black box, the behavior was encoded with regard to its physical properties (movement trajectory). Immediately afterwards, the subjects copied the choice of the agent, and interacted longer with this target object compared to the other object, but only if they had previously perceived the agent to behave in a goal-directed way. These results show that even

simple forms of social learning, such as stimulus enhancement, rely on goal-attribution in marmosets.

Finally, marmosets co-represent each other's actions when jointly engaged in a task (Joint Simon effect: Sebanz, Knoblich, & Prinz, 2003). In the individual Simon task, subjects have to react to a stimulus with a specific response while a second, conflicting stimulus prompts a response that is incompatible with the correct answer. In a situation where subjects can fully ignore the conflicting stimulus because it would only be relevant for a partner who is jointly engaged in the same task, humans nevertheless do not ignore this stimulus. This suggests that human subjects not only represent their own task and actions, but also their partner's, which is supported by neuroimaging studies (Wen & Hsieh, 2015). This Joint Simon effect appears rather late in human ontogeny and has been linked to Theory of Mind development (Milward, Kita, & Apperly, 2016). Recently, a joint Simon effect and thus action co-representation has been demonstrated in common marmosets (Miss & Burkart, in press). These results are consistent with their ease of coordinating activities, including vocal exchanges.

Taken together, callitrichid monkeys possess mirror neurons and show high-fidelity copying of behavior, have been shown to engage in social learning only if they perceive a behavior as intentional, and co-represent each others' behaviors in a joint task. The presence of these mechanistic elements stressed by the mirror system hypothesis suggests some fundamental parallels between human and callitrichid communication.

**5) TOWARDS A NEW ROADMAP**

We suggest that the cooperative breeding perspective on language evolution complements the MSH, by focusing on a critical gap in the old road map, i.e. the origin of the motivation to share information (see also Wacewicz et al.'s platform of trust, this issue), and by providing a working hypothesis for why it was the cooperatively breeding humans, rather than any other ape species to develop language.

The complexity of callitrichid vocal communication reviewed in this paper suggests that cooperative breeding indeed facilitates the evolution of more complex communication systems, and thus in the case of humans, of language. We have highlighted three potential pathways that may link cooperative breeding and vocal complexity: First and most importantly, the readiness to share food may extend to a readiness to share information; second, cooperative breeders may face more contexts in which it is vital to coordinate with and monitor group members and third, immatures

may need to engage caregivers and use vocal communication to do so. These pathways appear to indeed foster vocal complexity in callitrichids, but perhaps not in communicative complexity more generally. Since the MSH posits that the path to speech is indirect, this may raise a challenge for this hypothesis. To further explore this issue, it is thus crucial to also study callitrichid communication in the broad sense and from a multi-modal perspective, e.g. including gestural communication.

Whereas the proposed pathways find considerable empirical support, we also highlight that more systematic evidence is necessary. First, the details of callitrichid communication complexity needs to be further delineated, e.g. combinatoriality, the role of working memory (see also Aboitiz & Putt, this issue), differences and similiarities in vocal control and turn-taking between humans and callitrichids (see also Wacewicz et al, this issue), and non-vocal communication. Second and most crucially, more comparative evidence from a broader range of primates and other lineages is required to further evaluate the impact of cooperative breeding on communicative complexity. Such approaches should be based on broad phylogenetic comparisons (as done, for instance in MacLean et al., 2014 or Burkart et al., 2014), or targeted constrasts (MacLean et al., 2012, Burkart & van Schaik 2010). This has recently been achieved for birds, where comparative evidence from a large number of bird species revealed that cooperatively breeding species have larger vocal repertoires compared to independently breeding species (Leighton, 2017).

Together, the evidence reviewed in this paper suggests convergent evolution of communicative complexity in callitrichids and humans, both cooperative breeders. The enhanced cooperative and prosocial attitudes associated with cooperative breeding may thus give rise to the motivation to share not only food, but also information, which is largely lacking in great apes. The combination of this motivation to share information with strong cognitive abilities (as was the case in the human ancestors, but not in callitrichid monkeys) could then set the stage for language evolution in our lineage.

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